

Predicting hunting success on willow ptarmigan using bag statistics and distance sampling estimates

Thomas Vogler



Høgskolen i **Hedmark**

Master Thesis
at Faculty of Applied Ecology and Agricultural Sciences

HEDMARK UNIVERSITY COLLEGE

2013

Abstract

Willow ptarmigan is a popular game species for recreational hunting purpose throughout its range and long term harvest statistics are available for many areas. For the State owned land in Sweden hunting report rates are unusually high and provide a high level of information, including hunting effort, making this a unique dataset. In easy accessible hunting areas hunting pressure commonly is high, making monitoring and managing populations necessary.

During this study harvest data from all hunting areas within the County of Jämtland and population estimates from four long term monitoring areas from the County of Jämtland, Sweden, from 1996 – 2010 were analysed.

The aim of this study was to develop methods to predict the success of hunters based on previous years harvest data and results from the yearly ptarmigan counts prior to the start of the hunting season, to avoid over-harvesting. Further a method to calculate the amount of hunting possible to achieve a defined harvest level was developed. And last, a set of management options to reduce hunting pressure were assessed.

Adult density, proportion of successfully reproducing adults and average brood size explained most of the variance within bag size ($R^2_{adj.} = 0.72$). CPUE did not differ over time ($p=0.12$) and area ($p=0.12$) and allowed to calculate amount of hunting possible to achieve certain harvest rate. Observed amount of hunting was lower than the hunting limit in most cases. Excluding foreign hunters can reduce total harvest up to 40% (2008/2009) while reducing bag limit and shortening the hunting season will have a marginal effect on harvest. .

I suggest using adult density, proportion of successfully reproducing adults and average brood size to determine harvest levels rather than overall density. Calculating hunting levels should be done by using a fixed CPUE value which takes local fluctuations into account and allows a certain amount of hunting every year. I suggest that the reporting system for hunting results is revised so the effective amount of hunting can be calculated and used for management decisions.

Introduction

Bag statistics are collected for many species and areas worldwide and are used as proxy for population size and change (Trehella, 1899; Small, 1993; Nielsen and Petruson, 1995; Bender and Spencer, 1999; Matsuda et al., 2002; Merli and Meriggi, 2006). Examples can be found on willow ptarmigan (*Lagopus lagopus*) (Myrberget, 1974; Small et al., 1993; Hörnfeldt, 1978), red grouse (*Lagopus lagopus scoticus*) (Haydon et al., 2002) rock ptarmigan (*Lagopus muta*) (Nielsen and Petruson, 1995), tetranoids (Kvasnes et al., 2010), red fox (*Vulpes vulpes*) (Trehella, 1988, Gloor et al., 2001), roe deer (*Capreolus capreolus*) (Grøtan et al., 2005) and red deer (*Cervus elaphus*) (Mysterud et al., 2007), whereas in the latter case additionally the number of deer seen during the hunt was used besides bag counts. Although the possibility of using bag statistics has been evaluated concluding that bag size time series are a good indicator for the population dynamics of ptarmigan spp. (i.e. Cattadori et al., 2003, Broms et al. 2010, Kvasnes et al. 2010, Hansen et al 2013,), Willebrand et al. (2011) found that variation in hunting effort had a larger effect on bag size than variation in ptarmigan density.

Willow ptarmigan inhabit arctic, subarctic and subalpine tundras of North America and Northern Eurasia as well as heather moorlands in Great Britain (Storch, 2007). Wherever willow ptarmigan occur they usually are quite common, but densities can vary widely from only 1 bird per km⁻² to 200 birds per km⁻² (Hannon, et al., 1998). In Sweden adult density varies between 2.4 – 8.2 adults per km⁻² were (Hörnell-Willebrand, 2005) and the average breeding success measured in august in Jämtland varied between 2.5 – 5.0 (1997-2010) chicks per pair (Swedish Ptarmigan Monitoring Scheme, unpublished data). In the UK populations in some areas are high with up to 115 pairs per km⁻² mainly because of management measures such as predator control (Etheridge et al., 1997; Tharme, 2001), rejuvenation of heather moorlands through burning (Thirgood et al., 2000) and vermicide treatment to reduce parasites and increase breeding success (Newborn & Foster, 2002). The species is currently as least concern (BirdLife International, 2012).

Willow ptarmigan is a popular game species worldwide. During the hunting season 2011/2012 150'000 willow ptarmigan were shot in Norway (Statistics Norway, 2012). In Sweden the total harvest on state owned land was 35'200 willow ptarmigan of which 12'300 were shot in County Jämtland (County Administrative Board of Jämtland, unpubl. data) and 61'700 in Finnland (Official Statistics of Finnland, 2012).

Willow ptarmigan chicks are being parented by both the male and female including protection from predators, warming the young and leading chicks to appropriate foraging grounds (Hannon &

Martin, 2006). The strategy of ptarmigan to avoid predators or hunters is crouching (Brøseth & Pedersen, 2010) until the predator or hunter gets too close when the ptarmigan flush. Adults expose themselves by displaying to distract from their brood and therefore are at a higher risk to be shot (Asmyhr et al., 2012). Large broods are easier to detect compared to single adults, making successful reproducing adults more vulnerable to harvest compared to single adults (Asmyhr et al., 2012). After brood breakup from mid to late October, ptarmigan move to wintering areas (Smith, 1997).

In addition to reduce abundance, hunting can change the dynamics of populations (Besnard et al., 2010; Solberg et al., 1999). Willow ptarmigan populations are known to be cyclic and cycle lengths can vary from 3 up to 10 years (Watson & Moss, 1979). Since willow ptarmigan are quite common, they provide an important resource for different species, like gyrfalcon (*Falco rusticolus*) and goshawk (*Accipiter gentilis*) (Koskimies & Sulkava, 2011; Tornberg, 1997) that can follow the cycles of ptarmigan (Mossop, 2011, Tornberg et al., 2005; Barichello & Mossop, 2011, Falkdalen et al., 2011). So, ptarmigan can be considered a keystone species and changing their population dynamics can have an impact on a whole ecosystem (Mossop, 2011).

Before 1993 willow ptarmigan hunting on state owned land in Sweden was only available for less than 1'000 hunters. In 1993, 60'000 km⁻² of state owned land where opened to the public for small game hunting (Willebrand & Hörnell, 2001) and numbers of hunters increased to over 10'000 hunters per year. During the hunting season 2012/2013 a total of 9'000 hunting reports were handed in of which 32% were from foreign hunters. There are concerns that hunting pressure can lead to over harvesting of willow ptarmigan populations (Willebrand & Hörnell, 2001) and several studies have investigated the effect of harvesting willow ptarmigan (Smith and Willebrand, 1999, Willebrand & Hörnell-Willebrand, 2001; Pedersen et al., 2003; Sandercock et al., 2010). Smith and Willebrand 1999 found hunting to be mainly additive to natural mortality. Sandercock et al. (2010) concluded hunting to be partially compensatory to natural mortality and did not find any difference in survival between not hunted areas and areas with 15% harvest, but a lower survival at 30% harvest and suggest a harvest rate of 15% to prevent overharvesting. No effect of hunting on ptarmigan survival despite harvest levels in excess of 15% has been found in Sweden (County administrative board of Jämtland, unpubl. data). As a rule of thumb, hunting managers in Sweden generally allow three hunting days per km⁻² assuming an outtake of approximately 30% of the population. When the yearly ptarmigan counts report densities below five ptarmigan per km⁻² the number of hunting days per km⁻² often is reduced. When a hunting area is closed for public hunting, municipality residents are allowed to continue hunting.

To prevent over harvesting of ptarmigan populations the managing authorities need tools, like above, to allow them to limit the hunting if necessary. The closing of hunting areas as practiced in Jämtland in 2009/2010 because of low densities is one option. Other solutions could be to exclude foreign hunters, as currently discussed or reduce bag limit which currently is set at eight ptarmigan per hunter and day.

In 2004 a new administrative system for hunting was introduced where hunters had to activate a hunting permit before hunting for up to five days on the internet platform smavilt.se. Before being able to activate an additional permit, the result of the hunt had to be reported on the same platform within two weeks of the hunt (smavilt.se, 2012). For each day hunters report exact date and hunting unit as well as number of shot bird/species and age. In Addition to bag data hunters report nationality, making it possible to evaluate the effect of foreign hunters on the total harvest. . Municipality residents have to activate their yearly permits in the same manner as day permits. Hunters that fail to hand in their report are not allowed to hunt during the first weeks of the following hunting season (County administrative board of Jämtland, 2013).

In Sweden willow ptarmigan hunting is mainly carried out with shot guns over pointing dogs which flush the birds. The hunting season for willow ptarmigan in Jämtland lasts from the 25th of August until the end of February with a two week hunting ban between the 6th and the 20th of September because of moose hunting (County administrative board of Jämtland, 2013).

Population densities on state owned Land in Sweden are estimated yearly before the hunting season starts using line transects with distance sampling (Buckland et al., 2001). Distance sampling is a common method used for population estimates (Plumptre, 2001; Brown & Boyce, 1998; Marques et al., 2001; Hörnell-Willebrand et al., 2006; Newson et al., 2008, Brøseth et al., 2005).

Bag statistics do not represent the demography of willow ptarmigan populations because hunting is selective (Hörnell-Willebrand et al., 2006; Asmyhr et al., 2012). A hunter is more likely to encounter a brood than a single adult and to shoot a ptarmigan when encountering a brood then when encountering a single adult (Asmyhr et al., 2012). This means that when number of broods per km⁻² is high and most pairs have reproduced successfully, hence the proportion of adults with broods is high, hunting success should be high as well.

Catch Per Unit Effort (CPUE) is commonly used as an index to estimate fish abundance (Gillis & Peterman, 1998; Diele et al. 2005; Kaunda-Arara & Rose, 2004), but rarely used in wildlife management (Willebrand et al., 2011). There have been attempts to use CPUE as an index for abundance of willow ptarmigan but Willebrand et al. (2011) concluded that bag size produced better index for population density than CPUE.

In this study I use bag statistics from four hunting areas in the southern Swedish mountain range in the County of Jämtland. Willow ptarmigan populations have been monitored yearly since 1996. Report rates of bag data is usually high (95% in hunting season 2010/2011) making this a unique dataset to evaluate the impact of harvest of willow ptarmigan. The southern parts of the Swedish mountain range, including the study areas, are easy accessible from large cities in southern Sweden, resulting in high hunting pressure.

During this study I want to find out 1.) If results from the yearly ptarmigan counts in combination with information from previous years harvest data can be used to predict hunting success 2.) If it is possible to develop a set of management rules based on total density, breeding success and previous year's harvest data (catch per unit effort, CPUE and bag size) making it possible to set harvest levels that follow the monitoring results more in detail compared to today's management practice. 3.) Evaluate the impact of foreign hunters by calculating efficiency of hunters with different nationalities. 4.) Assess the effect of further management options by shortening the length of the hunting season or reducing the bag limit to evaluate the potential reduction in harvest.

Methods

Data sources

Monitoring data

For this study monitoring data (birds/km⁻²) and breeding success estimated in early august from the yearly counts on state owned land in the Swedish mountain range (1996-2011) was used. Well trained personnel using hunting dogs walk on predefined transect lines and flush the ptarmigan. The field personnel are trained to differentiate between adult and juvenile individuals, resulting in the total number as well as the number of adults and juveniles per flushed observation. Perpendicular distance from the exact spot the bird(s) were flushed, to the transect line was measured and analysed using distance sampling (Buckland et al., 2001) and the software package DISTANCE (Thomas et al., 2010). The data was used to calculate total number of birds in a hunting unit, density of adults and chicks respectively, reproductive success (measured as chicks/pair) and the proportion of successfully reproducing adults (adults observed with chicks compared to adults observed without chicks, hereafter: proportion of broods). A brood was defined as at least one adult with at least one chick.

Harvest data

Hunting reports for the corresponding years and hunting units as in the monitoring data as well as the harvest data from the whole county of Jämtland was analysed during this report. From the period prior to the introduction of the new management scheme (period one, 1996 - 2003), hunting reports available are a lot less detailed, as information from the reports has been summarised for hunting areas and years, than the harvest data from the period from 2004 – 2010 (period two). So the two periods were treated separately for statistical analysis. The harvest data was used to calculate the amount of birds harvested within an area divided by its size (hereafter bag size) and catch per unit effort (CPUE, birds harvested divided by the amount of hunting days used) as a measure of hunting success.

Data manipulation

For hunters failing to report the harvest an entry in the database was created when they activated their permit but no matching report exists. I further identified entries within the dataset with the most common error being two entries for the same hunter and day. One of those entries did not contain any information on the harvest and was deleted. Some hunters managed to hand in one report per species instead of per day and these reports were merged. Dog owners can obtain a

cheaper training license giving them the right to use their dog in the hunting area. As no harvest takes place when only training dogs, I excluded those reports from further analysis. I adjusted the hunting days (Equation 1) and harvest (Equation 2) as follows.

$$\text{hunting.days} - (\text{faulty.reports} + \text{dog.training}) \quad (\text{Equation 1})$$

$$\text{harvest} \times \left(\frac{\text{miss.reports}}{\text{hunting.days}} + 1 \right) \quad (\text{Equation 2})$$

The data for period one did only include the sum of harvested birds per area and year and could not be divided into birds harvested within different parts of the season. When using data from period two, bag statistics were limited to the period from the 25th of August until the 30th of September to reduce the influence of dispersal to wintering habitats.

Study Area and sample sizes

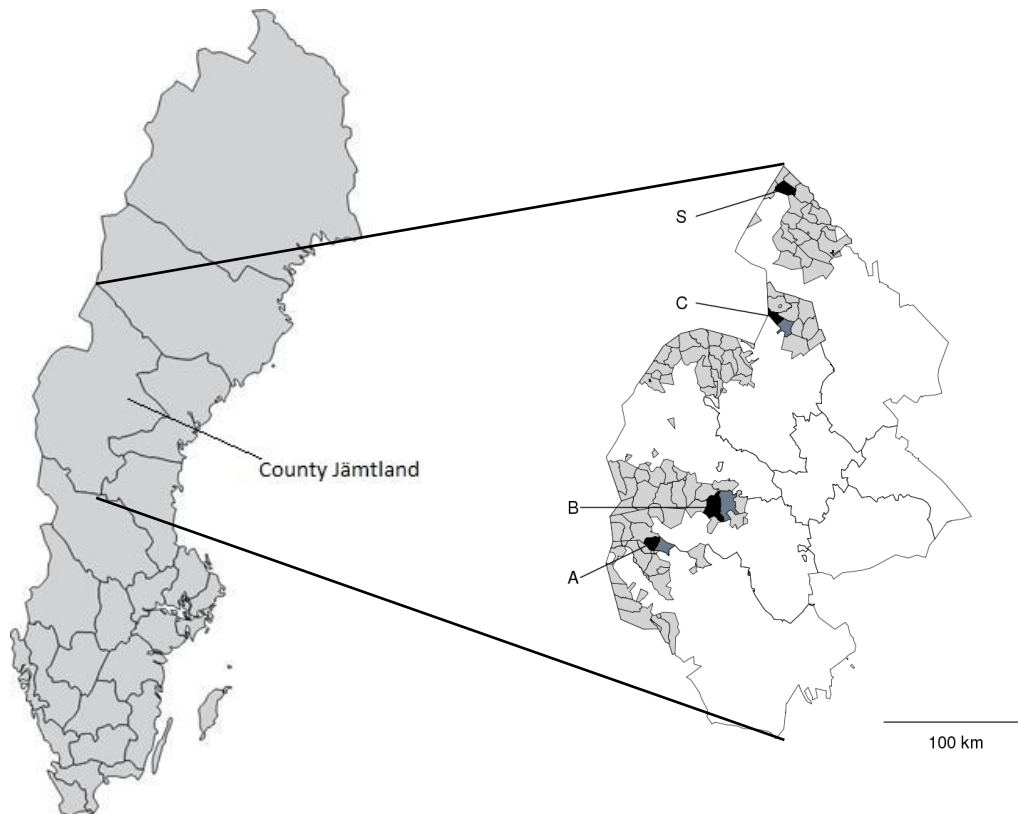


Figure 1: Map of Jämtland and its position within Sweden. A-C and S are the monitoring areas, part of a hunted area (black) and non-hunted control area (dark grey)

The data was collected from four ptarmigan monitoring areas in the county of Jämtland, Sweden (Figure 1). For period one there are four areas with eight years of data. Distance sampling monitoring for area D started in 1999 so there was no data available for the previous years,

resulting in a sample size of 29. The dataset of period two contains four areas with seven years of data. Hunting was closed during season 2009/2010 in all monitoring areas and during season 2010/2011 in area B. The sample size for period two is therefore 23.

*Table 1: Data summary for period two, stratified by area, presentet as mean (2*SE).*

Area	Adult density (ptarmigan km ⁻²)	Breeding success (chick per pair)	Bag (ptarmigan km ⁻²)	CPUE	Harvest rate
A	5.56 (2.33)	4.37 (0.46)	3.68 (1.21)	1.41 (0.51)	0.23 (0.08)
B	8.57 (3.48)	3.76 (1.28)	2.67 (0.63)	1.76 (0.36)	0.14 (0.05)
C	5.07 (1.90)	3.40 (1.11)	1.62 (0.69)	1.38 (0.37)	0.13 (0.05)
S	4.07 (0.66)	4.03 (1.42)	1.87 (0.97)	1.07 (0.43)	0.14 (0.03)

Modelling

Shapiro-Wilks tests were used to check the model parameters for normal distribution. When the test showed evidence for non-normal distribution the data was $\ln(1+x)$ transformed.

The mean ± 2 standard error of CPUE and bag size were calculated to check for significant differences between period one and two. Additionally a two-tailed independent sample Students T-Tests was conducted to check for compatibility of the two datasets.

To check for confounding effects among the model parameters the variance inflation factor (VIF) method was used. VIF is a measurement for multicollinearity between independent variables (Allison, 2012) and measures how much the variance of the estimated coefficients are increased over the case of no correlation among the X variables. If no variables are correlated, then all the VIFs will be 1 and it is a common practice to exclude variables from a model when VIF values are high. Definition of high can vary from 4, 10 to 30 (O'Brien, 2007).

Linear models (LM) were used to predict the hunting success (CPUE and bag size). A backward selection on the remaining, non-confounded predictors was carried out removing least significant variables according to p-values. Additionally, a level two automated model selection with the R-package glmulti was conducted. Glmulti runs every possible unique model including the specified variables as well as their pairwise interaction at level two (Calcagno and Mazancourt, 2010). Models were ranked according to the Akaike information Criterion (AIC) (Akaike, 1973).

All statistical computing was carried out in R (R Development Core Team, 2012), data manipulation was done in Excel.

Calculating stable harvest levels

The temporal and spatial variation of CPUE and bag size were analysed to assess the possibility to be used as a fixed parameter when calculating the maximum amount of hunting possible, at a certain harvest level. Temporal and spatial stability were checked by using one way ANOVA with years and area-id as independent groups. Analysis was carried out on the data from period two only. The fixed value of CPUE was then used to calculate the amount of hunting days (*Equation 3*) to achieve a harvest level of 30% and compared to the observed and the fixed amount of 3 hunting days per km⁻².

$$\frac{density \times harvest.rate}{fixed_parameter} \cong huntingdays \text{ (Equation 3)}.$$

Possible management options

To investigate the impact of hunters according to their nationality, data from period two was used from all hunting areas in Jämtland. Nationality of hunters was classified into Swedish, Nordic and non-Nordic hunters, where Nordic hunters are defined as Finnish, Danish and Norwegian hunters and non-Nordic as hunters from other EU-member states. Average bag size was used to compare the efficiency of hunters. To evaluate the impact of foreign hunters on total harvest, harvest by nationality class were compared to total harvest.

To assess the influence of shortening the hunting season, total harvest was categorised by month for the years in period two.

To assess the effect of reducing bag size of willow ptarmigan on total harvest, hunting reports were categorised by number of bagged ptarmigan. The potential reduction in total harvest was calculated, by reducing reports with higher number of ptarmigan shot to the theoretical bag limit for the years in period two.

Results

The return rate of hunting reports was between 86 – 96% and return rate was highest in recent years, except for the seasons 04/05 and 05/06 where no, or only very few reports were missing. An average missing report rate from the seasons 06/07 – 10/11 was used to adjust the seasons 04/05 and 05/06 (*Appendix B*).

CPUE and bag size did not differ between period one and two (*Figure 2*), $df=34.8$, $t=0.33$, $p=0.74$ and $df=40.2$, $t=1.76$, $p=0.08$ respectively. However, there seems to be a trend for lower bag sizes in period two that could be the result of the inaccuracy in the data from period two. I therefore chose to continue the analysis only using data from period two.

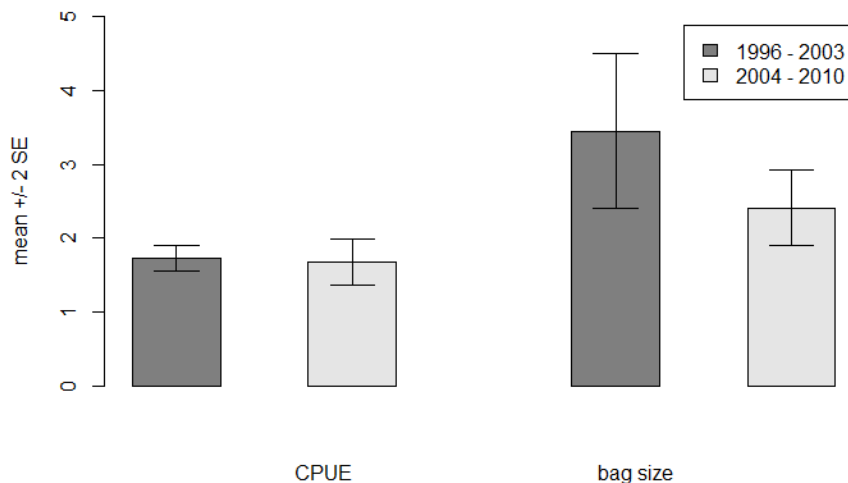


Figure 2: comparison between time period 1996-2003 and 2004-2010 using the means of CPUE and bag size $\pm 2 \cdot SE$

Results from the Shapiro-Wilks tests showed a normal distribution on both response variables CPUE ($p=0.10$) and bag size ($p=0.24$). The predictors chicks per pair ($p=0.77$), proportion of broods ($p=0.15$) and average brood size were normal distributed. Total density ($p=0.04$), adult density ($p=0.03$), chick density ($p=0.04$) and brood density ($p<0.01$) were not normal distributed and were $\ln(1+x)$ transformed (*Table 2*).

Table 2: Shapiro-Wilks test of all model parameters, data from period two

Variable	W	p	W transf.	p transf.
CPUE	0.929	0.104	-	-
total density	0.9117	0.04426	0.9668	0.6138
chick per pair	0.9736	0.7734	-	-
adult density	0.9061	0.03388	0.9713	0.7206
chick density	0.9113	0.04341	0.9741	0.785
brood density	0.8769	0.008719	0.9282	0.09986
proportion of broods	0.9373	0.1572	-	-
average broodsize	0.9476	0.2604	-	-
Bag size	0.9455	0.2354	-	-

Total density (VIF=1249) was most confounded with the other parameters in the model. Since adult density + chick density equals total density and both adult density ($r=0.88$) and chick density ($r=0.93$) (Figure 3) were highly correlated with total density, total density was removed from the model. Besides producing the highest VIF values (VIF=346), brood density was highly correlated with chick density ($r=0.95$) and adult density ($r=0.79$) (Figure 3) and was removed from the analysis. Remaining VIF values were still high (VIF(chick density)=16), but since the amount of chicks in a population is important for the hunting success, no further variables were excluded from the model.

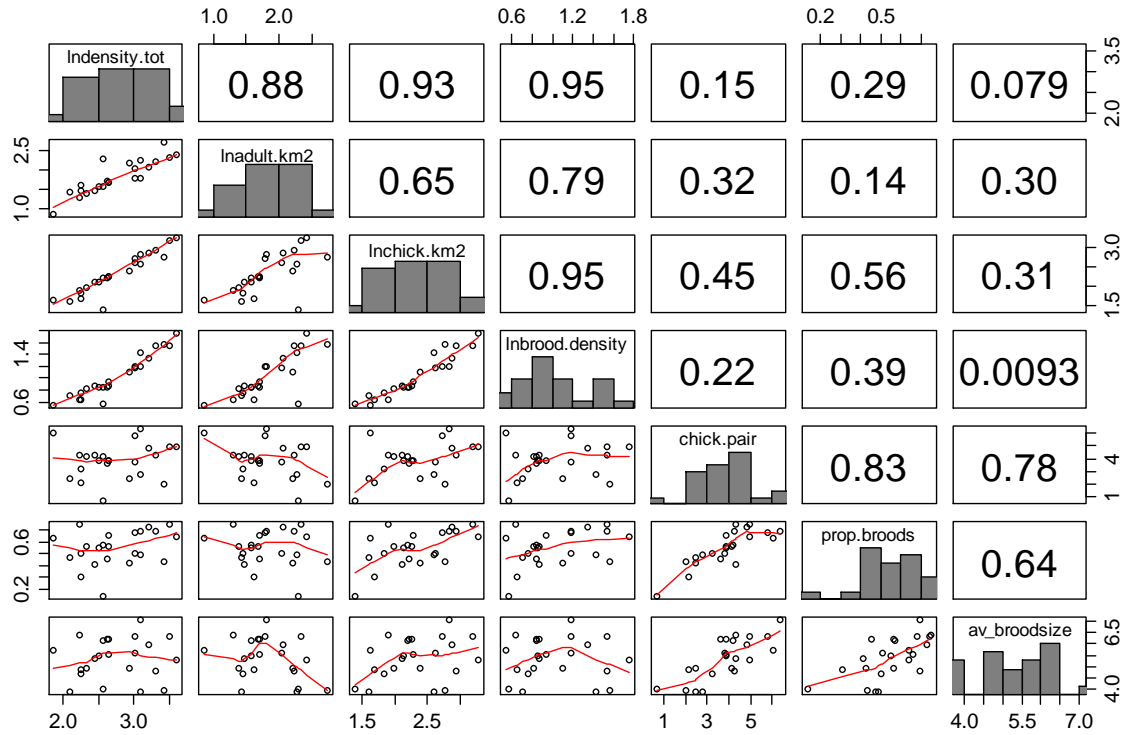


Figure 3: correlation matrix of predictor variables

Predicting hunting success measured as CPUE

Linear regression models using CPUE as a response variable were fitted. Average brood size ($p=0.72$, $R^2_{adj}=-0.04$), chicks per pair ($p=0.39$, $R^2_{adj}=-0.01$) and proportion of broods ($p=0.23$, $R^2_{adj}=0.02$) are not significant and explain very little of the variation of the dataset. Chick density ($p<0.001$, $R^2_{adj}=0.52$) and adult density ($p=0.002$, $R^2_{adj}=0.34$) both were significant (Figure 4).

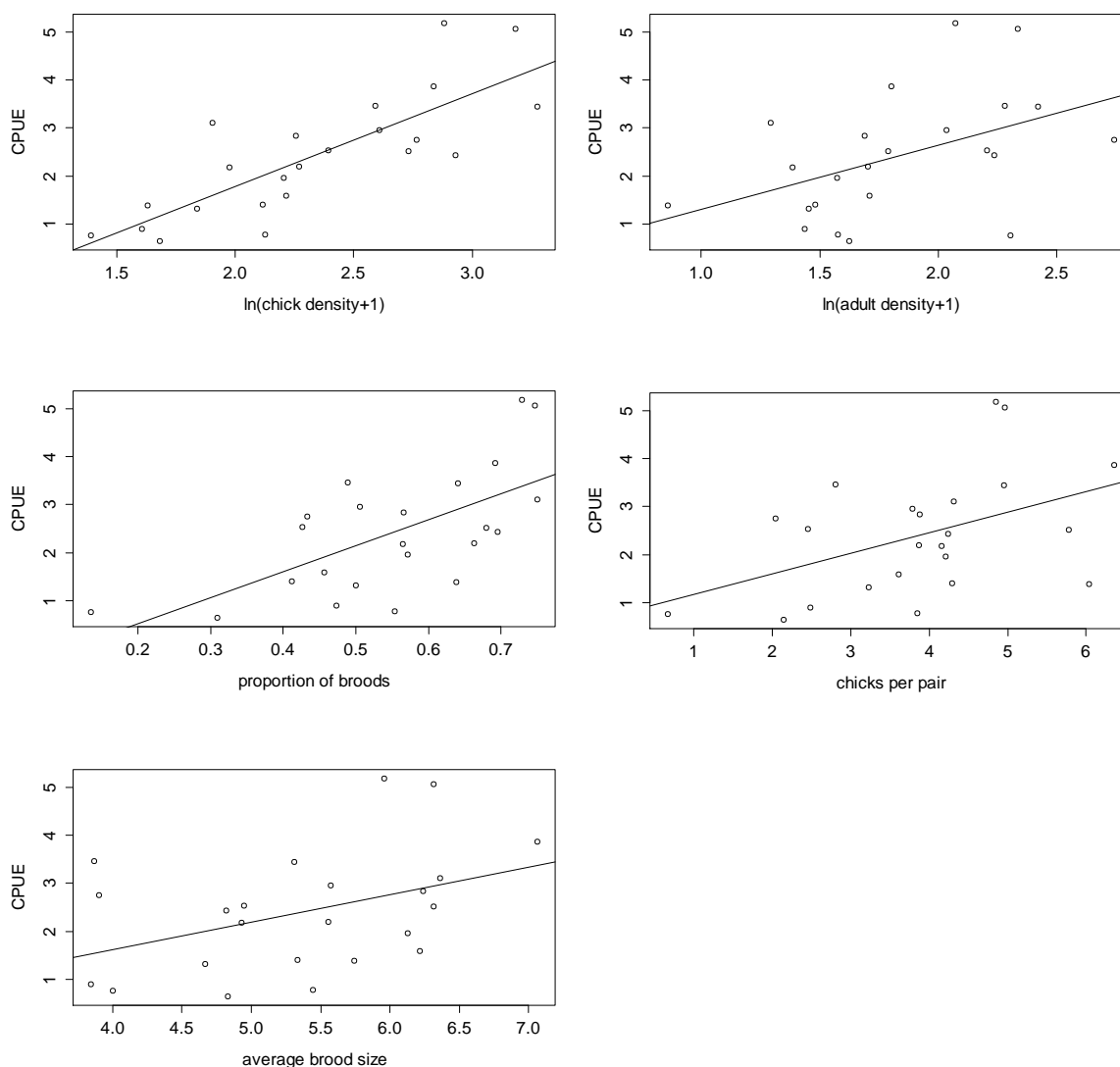


Figure 4: Regressions of all model parameters toward the response variable CPUE. Data from period two from the four monitoring areas in county Jämtland. Chick density and adult density are $\ln(1+x)$ transformed. Values are observed, not model predicted

The full model without any interactions was fitted first. A backward selection eliminated adult density ($p=0.96$), chick per pair ($p=0.97$), average brood size ($p=0.70$) and proportion of broods ($p=0.20$) from the full model. The model using only chick density ($p<0.01$, $R^2_{adj}=0.52$) was the result of the backward selection. However, according to R^2_{adj} values, the model including chick density and proportion of broods performed better ($p<0.01$, $R^2_{adj}=0.54$). A level one analysis with glmulti resulted in the same two models to perform best. The best model on a level two glmulti analysis included all five variables as well as four interactions. As such a complex model is hard to interpret, a model including chick density, adult density chick per pair and the interaction between adult density and chick per pair (which was among the best ranked models from the glmulti output) was used instead. A model using adult density, proportion of adults with broods and average brood size

was included as a candidate model (*Table 3*). Chick density as single predictor remained the best model according to AIC values.

Table 3: candidate models for the period 2004 - 2010 using CPUE as response variable ranked by AIC value

Rank	model parameters; Response=CPUE	Dev.	R ² adj.	AIC	d AIC
1	Chick density	2.77	0.52	22.56	0.00
2	Chick dens. + adult dens. + chick per pair +(adult dens.*chick per pair)	2.18	0.56	23.07	0.51
3	Chick dens. + av. broodsize	2.62	0.53	23.28	0.72
4	Adult dens. + chick dens. + av. brood size + prop. of broods + chick per pair	2.53	0.46	28.49	5.93
5	Adult dens. + prop. of broods + average broodsize	3.04	0.42	28.74	6.18

Predicting hunting success measured as bag size

Linear regression models were fitted with bag size as response variable. All the parameters were significant; chick density ($p < 0.001$, $R^2_{adj} = 0.62$), proportion of broods ($p < 0.001$, $R^2_{adj} = 0.39$) ($p < 0.001$) adult density ($p = 0.02$, $R^2_{adj} = 0.18$), chicks per pair ($p = 0.03$, $R^2_{adj} = 0.17$) and average brood size ($p = 0.05$, $R^2_{adj} = 0.13$) (*Figure 5*).

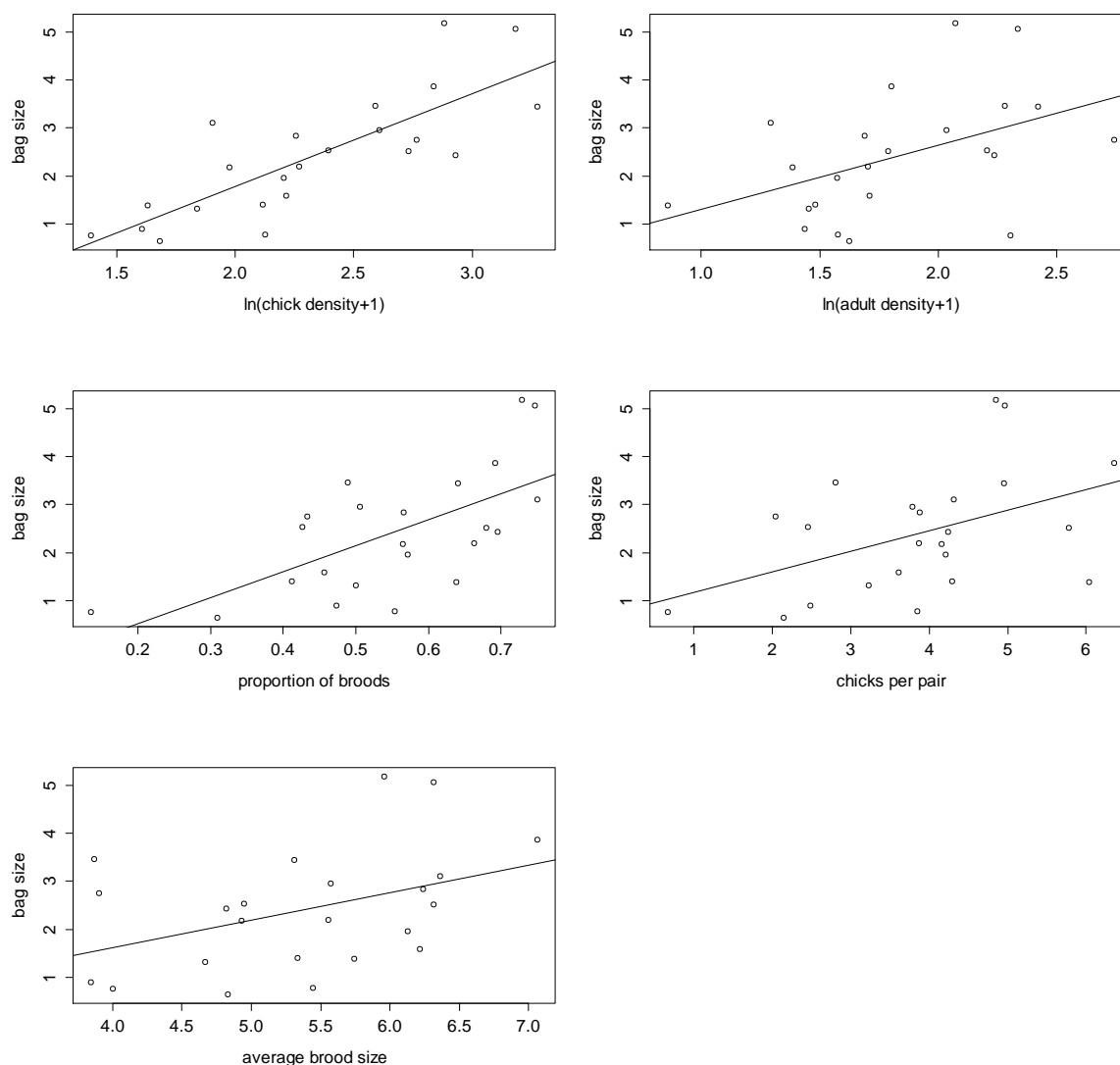


Figure 5: Regressions of all model parameters toward the response variable bag size. Data from period two from the four monitoring areas in county Jämtland. Chick density and adult density are $\ln(1+x)$ transformed. Values are observed, not model predicted

The full model without any interactions was fitted first. A backward selection eliminated the variables chick per pair ($p=0.96$), chick density ($p=0.89$) and average brood size ($p=0.15$) resulting in the model using adult density and proportion of broods as predictors ($p<0.01$, $R^2_{adj}=0.71$). Adding average brood size to that model improved the model fit slightly ($p<0.01$, $R^2_{adj}=0.72$). Glmulti showed the same results when only using additive models. Including interactive effects in the automated model selection, produce two models with an acceptable number of variables (<5). The model with adult density, average brood size and proportion of broods performed best. The second adds the interaction between proportion of broods and average brood size to that model. Adding

interactions did not improve the model fit according to AIC values but slightly increased the adjusted R-squared value (Table 4).

I calculated the VIF values for the highest ranked model. There is no sign of confounding effects ($VIF < 2$). Calculating the VIF for the second best model showed high values ($VIF(\text{av. Brood size} * \text{prop. Of broods}) = 90$), which is to be expected when including interactions and can be ignored (Allison, 2012).

Table 4: candidate models for the period 2004-2010 using bag size as response variable ranked by AIC values

Rank	model parameters; response = bag size	Dev.	R ² adj.	AIC	d AIC
1	Adult dens. + av. broodsize + prop. of broods	8.34	0.72	51.93	0.00
2	Adult dens. + av. Broodsize + prop. of broods + (av. brood size*prop. of broods)	7.77	0.73	52.30	0.37
3	Adult dens. + prop. of broods	9.31	0.71	52.48	0.55
4	Adult dens. + chick dens. + av. brood size + prop. of broods + chick per pair	8.33	0.69	55.91	3.98

Calculating stable harvest levels

Bag size did not show any difference between years ($F(5, 17) = 1.32$, $p = 0.30$), but between areas ($F(4, 24) = 13.60$, $p < 0.001$). CPUE did not show any significant difference, over time ($F(5, 17) = 2.09$, $p = 0.12$) or between areas ($F(4, 24) = 2.20$, $p = 0.12$). The mean of CPUE ($=1.40$) was defined as fixed parameter to calculate hunting days. Calculated number of hunting days for a harvest level of 30% was higher than the management limit of three hunting days per km^{-2} at high densities (>14 ptarmigan/ km^{-2}) and lower at medium densities (5-15 ptarmigan/ km^{-2}). At low densities (<5 ptarmigan/ km^{-2}), when hunting areas were closed calculated hunting still allows for a low amount of hunting (Figure 6). Observed average harvest rate excluding years without hunting was 15.72% ($n=23$).

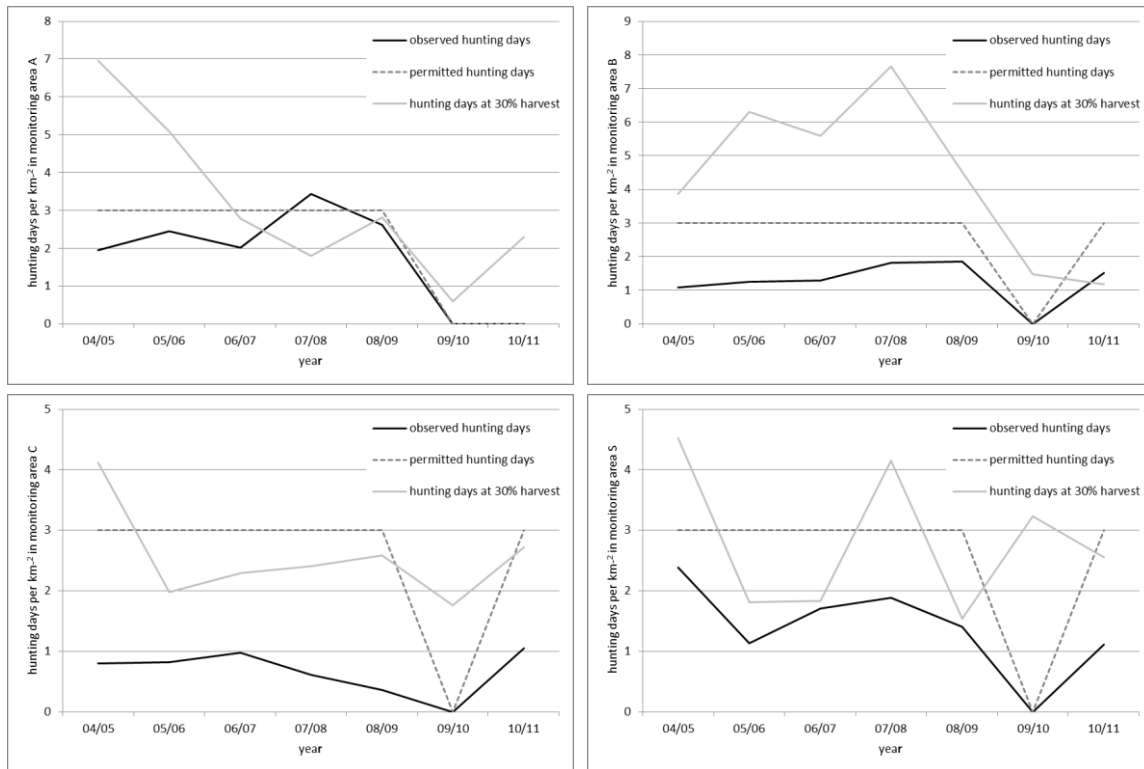


Figure 6: Observed, permitted and calculated (with a harvest level of 30%), amount of hunting days in monitoring areas A-C and S from 2004-2010

Hunting over time

57 – 70% of harvest occurs during the first week of hunting in August (excluding the hunting season 09/10 as it is not representative for an average hunting season). Only 1 – 1.7% of harvest occurs during two month period from January - February (Figure 7). To effectively reduce the amount of hunting, the season would have to be shored down to two weeks.

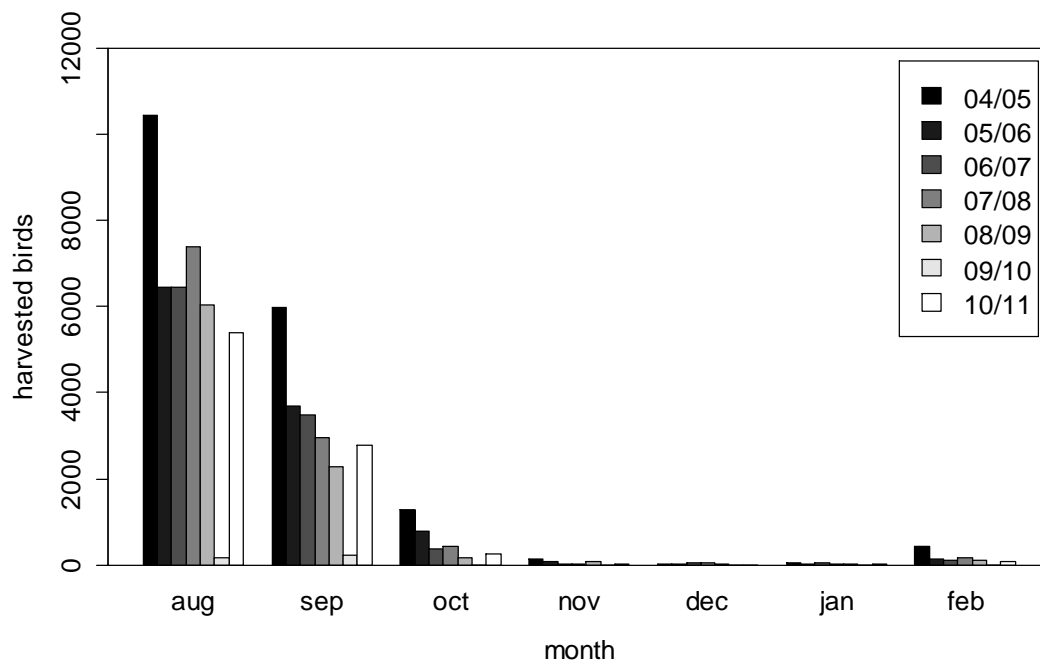


Figure 7: total harvested birds from all hunting areas in county Jämtland per month for the entire hunting season from 2004 – 2010

Origin of hunters

Nordic hunters were significantly more efficient than Swedish hunters in most hunting seasons (04/05, 07/08, 08/09, and 10/11) with an average of 1.05 compared to 0.8 bagged ptarmigan and less efficient in season 09/10. Non-Nordic hunters have a trend to be more efficient and were most efficient in the hunting season 05/06 and 08/09 with an average of 1.22 bagged grouse compared to Swedish (0.72) and Nordic hunters (0.81) (Figure 8). During the years 2004-2010 foreign hunters took out 19%-38% of the total harvest, with Nordic hunter being responsible for 14-35%, non-Nordic hunters for 1-11% and Swedish hunters for 61%-84% of total harvest (Figure 9).

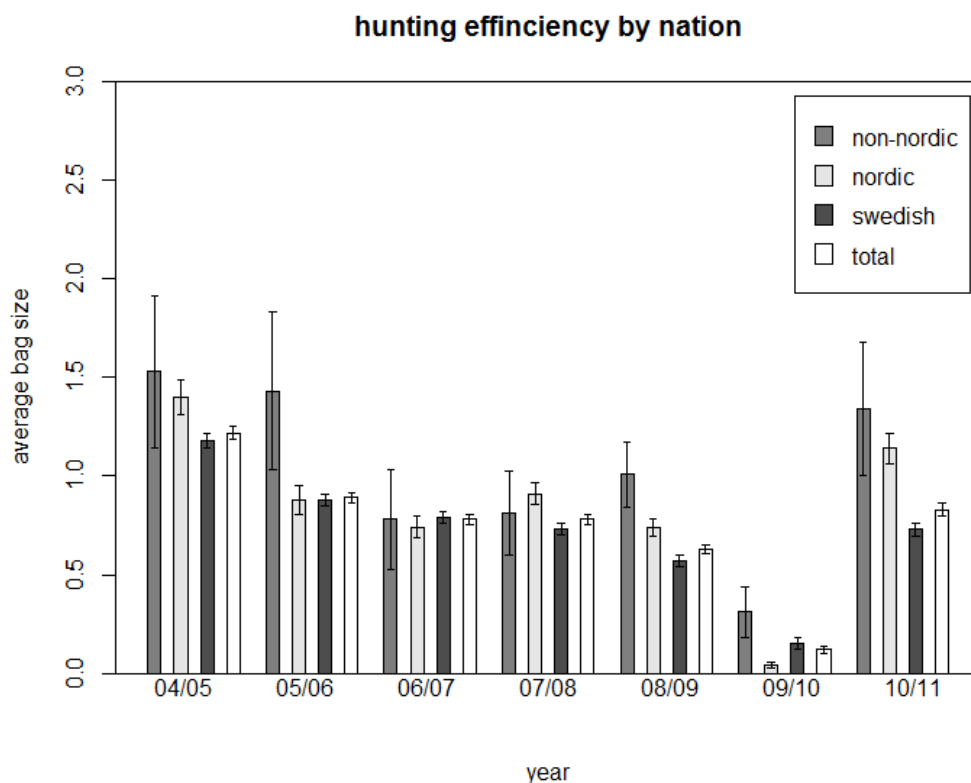


Figure 8. Average bag size \pm 2 standard errors of hunters classified by nationality from 2004-2010 from all hunting areas of Jämtland

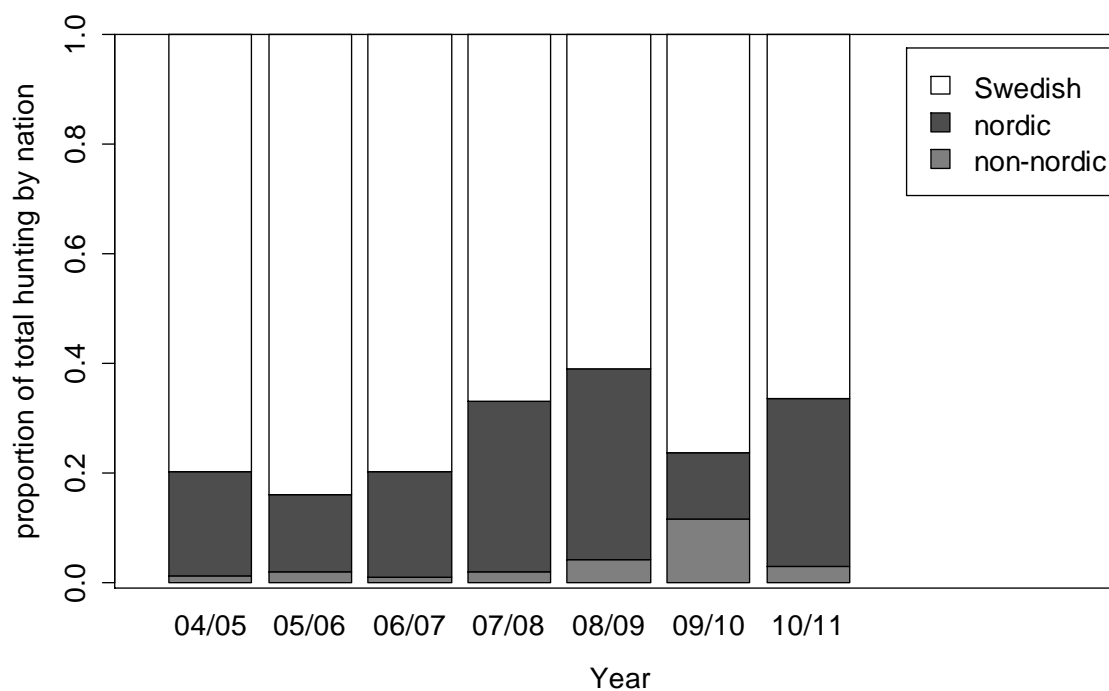


Figure 9: Proportion of total harvest by nationality group from 2004-2010 from all hunting areas of Jämtland

Reducing bag limit

Reducing bag limit would have a small effect as only 1.4% of hunters managed to shoot eight ptarmigan in a day during the years 2004 – 2010. For example in the Season 04/05 which had the highest average bag size, a reduction of the bag size down to six instead of eight, which equals a reduction of 25% would have reduced the total harvest only by 4 %. In the same season the majority of handed in reports (59%) did not report any harvested ptarmigans at all. The summarized harvest from 2004-2010 shows a potential reduction of total harvest by 21% when bag limit is reduced to three ptarmigan per hunting day (*Figure 10*).

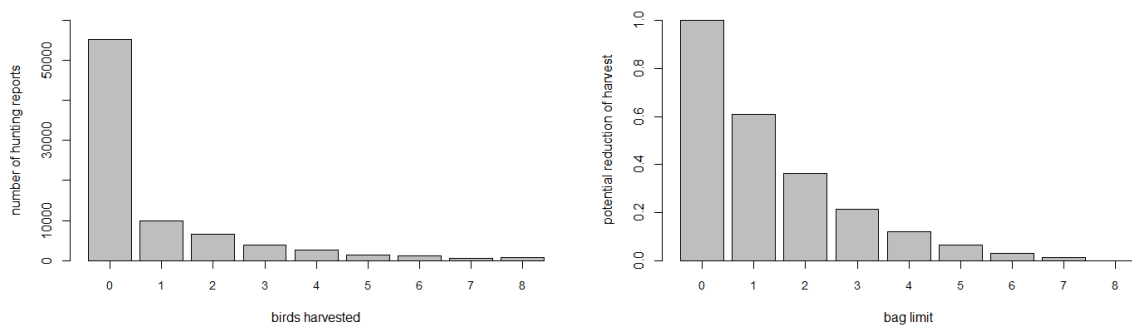


Figure 10: number of bagged ptarmigan per hunting report and potential reduction of total harvest at different bag limits during 2004-2010

Discussion

In this study I show that bag size was the better estimate for hunting success than CPUE, derived from monitoring data, and that the variables adult density, proportion of broods and average brood size predicted bag size best. I further developed a more accurate, region specific, way to calculate the amount of hunting possible given a certain pre-defined harvest level. Limiting hunting to Swedish residents would be an effective way to reduce total amount of harvest but lowering the bag limit and shortening the hunting season do not help to reduce the total amount of hunting.

Comparing the two time periods of the dataset didn't show any significant differences in bag size or CPUE. However, there seems to be a trend for lower bag size in period two. An assumption that mainly unsuccessful hunters failed to hand in hunting reports, would lead to an overestimation of average bag size. Average bag size was used to correct total harvest for missing hunting reports and could explain the trend for higher harvest rates in period one.

The amount of hunting reports handed in was high, with highest rates during recent years, except for the seasons 04/05 and 05/06 when missing hunting reports were <1%. I do not believe that the report rate was higher during those years than it is today, as hunters have become more accustomed to the new report system and punishment for failing to hand in reports has become stricter.

Asmyhr et al., 2012 showed that successfully reproducing adults with large broods are most vulnerable to harvest and hunters should be more effective under such conditions. Also, high densities with a low adult and high chick density would lead to increased hunting success. This makes adult density, chick density, proportion of broods, average brood size, and chicks per pair important variables when calculating hunting efficiency

Predicting hunting success

Using bag size as response resulted in a better model fit as when using CPUE. CPUE is not much used in harvest management. However, CPUE includes hunting effort which explains most variation of willow grouse density. Further amount of hunting in today's management practice is measured as effort per day and using the amount of shot birds per day should be reflected in hunting success. CPUE is varied less than bag size and can be used as a fixed value for calculating harvest. I would have expected CPUE to produce better models if hunter would act as true predators and increase harvest with increased density. Willebrand et al., (2011) showed that hunting effort was the more important factor influencing bag size than density and hunters take out a larger proportion of the population at lower densities. Wam et al. (2013) found that 43% of hunters questioned valued the

recreational aspect of the hunt higher than the harvest itself. However, the management practice in Sweden today is to lower number of hunting days per km⁻² when densities are low.

When doing simple regressions, CPUE increased with 1.10 and bag size with 5.84 when increasing chick density by one and with 1.06 and 2.77 respectively when increasing adult density. An increase of 0.1 in proportion of broods CPUE increased with 0.09 and bag size with 0.58. Increasing chick per pair by one increased CPUE by 0.43 and bag size by 0.07. Average brood size by itself also showed a low connection when increased by 1 with a CPUE and bag size increase of 0.05 and 0.57 respectively.

A linear model using the variables adult density, proportion of broods and average brood size explained bag size best. By using this model it will be possible to identify when hunting success could be high. Taking into account density levels management decisions on harvest levels can be made. However, not all managing authorities will have the expertise to put the information of this model into use. Further, the time between autumn population counts and start of the hunting season is short and does not leave much time for analysis and making management decisions. Also does this way of determining harvest require distance sampling counts which for smaller hunting units may not be available and affordable in case of independent land owners. These management suggestions underlie the assumption that harvest pressure is high and has to be regulated. This is the case for Jämtland, especially the southern parts but more rural areas where the harvest limit is never reached, such an extensive management will not be necessary.

Encounters are more important than overall densities for hunting success and encounters with large broods are more likely, because of increased detectability by hunting dogs (Asmyhr et al., 2012). A scenario A) with low adult density, high average brood size and high proportion of broods and a scenario B) with high adult density, low average brood size and low proportion of broods would lead to similar high densities. However, in scenario B) hunting success will increase and the possibility of overharvesting is higher. By making management decisions solely based on total density as today, such differences are not taken into account. I suggest that breeding success is taken into account when determining the amount of hunting.

Calculating accurate hunting days

I used a fixed county wide CPUE value to calculate the amount of hunting possible instead of using the same amount of hunting days at any level of density (except below five ptarmigan per km⁻²) or breeding success. Since the densities and breeding success in the four monitoring areas are representative for a larger region (Hörnelli-Willebrand unpubl. Data), a region specific amount of hunting can be allowed. This would allow a small amount of hunting even at very low density levels.

I suggest more attention is paid to the reported hunting data. Areas were closed under the assumption that the hunting limit of three hunting days per km⁻² is reached. However, after cleaning the data from faulty reports, double registration and activated but unused day-permits, the observed number of hunting days is lower than the permitted in most cases. While this is not a problem from a biological perspective, more hunting would be possible, resulting in a loss of income for the managing authorities

Influence of foreign hunters

Foreign hunters, Nordic and non-Nordic are more efficient than Swedish hunters in most years. Swedish hunters were never most efficient during the years analysed, but more efficient than Nordic hunters during hunting season 09/10, during which most hunting areas were closed and therefore is not representative for an ordinary hunting seasons. Non-Nordic hunters have a tendency to be most efficient but only account for a small proportion of total harvest.

Other management options

Shortening hunting season and lowering bag limit would have to be severe to have any effect on harvest levels and are probably not a valid management option because of political issues. There also is possibility that hunters do not follow the bag limit once they have the chance to harvest more.

Management implication

Rather than using a total density level of five birds per km^{-2} , managers should take breeding success into account and calculate numbers of bird contacts per km^{-2} when deciding on lowering the amount of hunting days or closing an area. This would adjust for situations where there are very few large broods and hunting success probably is high. For example an area with an average brood size of seven and a density of 14 birds per km^{-2} would only result in two bird contacts. An average brood size of 3 and a density of 15 birds per km^{-2} would result in five bird contacts an probably lower hunting efficiency and lower risk of over harvesting at similar densities.

Acknowledgements

First I would like to thank Maria Hörnell-Willebrand for all her support and help as well as patience while writing this master thesis. Further, I am grateful to the county board of Jämtland for letting me use the data from the distance sampling counts and the vast database of hunting reports. My thanks also go to the numerous volunteers who collected all the data and made this report possible. At last I would like to thank my family and friends for their support and help during my studies.

Evenstad, 14.05.2013

A handwritten signature in blue ink, appearing to read 'T. Vogler', with a stylized, cursive flourish at the end.

Thomas Vogler

References

- County administrative board of Jämtland. (2013, 05 10). Retrieved from <http://www.notisum.se/rnp/sls/lag/19870905.HTM>
- Akaike, H. (1973). Information theory and an extension to the maximum likelihood principle. In B. N. (Petrov, & F. Czaki (Ed.), *2nd International Symposium on Information Theory*, (pp. 267-281). Budapest: Akademiai Kiado.
- Allison, P. (2012). *Statistical Horizons*. Retrieved 04 12, 2013, from <http://www.statisticalhorizons.com/multicollinearity>
- Asmyhr, L., Willebrand, T., & Hörnell-Willebrand, M. (2012). Successful adult willow grouse are exposed to increased harvest risk. *The Journal of Wildlife Management*(76), pp. 940–943.
- Barichello, N., & Mossop, D. (2011). The Overwhelming Influence of Ptarmigan Abundance on Gyrfalcon Reproductive Success in the Central Yukon, Canada. *Gyrfalcons and Ptarmigan in a Changing World – Conference Proceedings*, pp. 307–322.
- Bender, L. C., & Spencer, R. D. (1999). Estimating Elk Population Size by Reconstruction from Harvest Data and Herd Ratios. *Wildlife Society Bulletin*, 27(3), pp. 636-645.
- Besnard, A., Novoa, C., & Gimenez, O. (2010). Hunting impact on the population dynamics of Pyrenean grey. *Wildlife Biology*(16), pp. 135-143.
- BirdLife International. (2012). *Lagopus lagopus*. Retrieved November 2., 2012, from IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2.: www.iucnredlist.org
- Broms, K., Skalski, J. R., Millspaugh, J. J., Hagen, C. A., & Schulz, J. H. (2010). Using Statistical Population Reconstruction to Estimate Demographic Trends in Small Game Populations. *The Journal of Wildlife Management*, 2, pp. 310–317.
- Brøseth, H., & Pedersen, H. C. (2010). Disturbance effects of hunting activity in a willow ptarmigan *Lagopus*. *Wildlife Biology*(16), pp. 241-248.
- Brøseth, H., Tufto, J., Pedersen, H. C., Steen, H., & Kastedalen, L. (2005). Dispersal patterns in a harvested willow ptarmigan population. *Journal of Applied Ecology*(42), pp. 453–459.
- Brown, J. A., & Boyce, M. S. (1998). Line transect sampling of Karner blue butterflies (*Lycaeides melissa samuelis*). *Environmental and Ecological Statistics*, 5, pp. 81-91.

- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introuction to Distance Sampling*. Oxford University Press.
- Calcagno, V., & Mazancourt, C. (2010). glmulti: An R Package for easy Automated Model Selection with (Generalized) Linear Models. *Journal of Statistical Software*(34).
- Cattadori, I. M., Haydon, D. T., Thirgood, S. J., & Hudson, P. J. (2003). Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. *Oikos*(100), pp. 439-446.
- County administrativ board of Jämtland. (2013, 5 10). *Länsstyrelsen Jämtlands län*. Retrieved from <http://www.lansstyrelsen.se/jamtland/En/Pages/default.aspx>
- Diele, K., Koch, V., & Saint-Paul, U. (2005). Population structure, catch composition and CPUE. *Aquatic Living Resources*(18), pp. 169-178.
- Etheridge, B., Summers, R. W., & Green, R. E. (1997). The Effects of Illegal Killing and Destruction of Nests by Humans on the Population Dynamics of the Hen Harrier *Circus cyaneus* in Scotland. *Journal of Applied Ecology*(34), pp. 1081-1105.
- Falkdalen, U., Hörnell-Willebrand, M., Nygård, T., Bergström, T., Lind, G., Nordin, A., & Warensjö, B. (2011). Relations Between Willow Ptarmigan (*Lagopus lagopus*) Density and Gyrfalcon (*Falco rusticolus*) Breeding Performance in Sweden. *Gyrfalcons and Ptarmigan in a Changing World – Conference Proceedings*, pp. 171-175.
- Gillis, D. M., & Peterman, R. M. (1998). Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. *Canadian Journal of Fisheries and Aquatic Sciences*(55), pp. 37-46.
- Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P., & Breitenmoser, U. (2001). The rise of urban fox populations in Switzerland. *Mammalian Biology*(66), pp. 155-164.
- Grøtan, V., Sæther, B.-E., Engen, S., Solberg, E.-J., Linnel, J. D., Andersen, R., . . . Lund, E. (2005). Climate causes large-scale spatial synchrony in population. *Ecology*(86), pp. 1472-1482.
- Hannon, S. J., & Martin, K. (2006). Ecology of juvenile grouse during the transition to adulthood. *Journal of Zoology*(269), pp. 422-433.
- Hannon, S. J., Martin, K., & Eason, P. K. (1998). The Willow Ptarmigan. In A. Poole, & F. Gill, *The Birds of North America* (Vol. 369). Philadelphia, PA: The Birds of North America, Inc.

- Hansen, B. B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., . . . Pedersen, Å. Ø. (2013). Climate Events Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic. *Science*, 6117, pp. 313-315.
- Haydon, D. T., Shaw, D. J., Cattadori, I. M., Hudson, P. J., & Thirgood, S. J. (2002). Analysing noisy time-series: describing regional variation in the cyclic dynamics of red grouse. *The Royal Society*(269), pp. 1609-1617.
- Hörnne-Willebrand, M. (2005). Temporal and Spatial Dynamics of Willow Grouse *Lagopus lagopus*. *Swedish University of Agricultural Sciences, doctoral thesis*.
- Hörnne-Willebrand, M., Marcström, V., Brittas, R., & Willebrand, T. (2006). Temporal and spatial correlation in chick production of willow grouse *Lagopus lagopus* in Sweden and Norway. *Wildlife Biology*(12), pp. 347-355.
- Hörnfeld, B. (1978). Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia*(32), pp. 141-152.
- Kaunda-Arara, B., & Rose, G. A. (2004). Effects of marine reef National Parks on fishery CPUE in coastal Kenya. *Biological Conservation*(118), pp. 1-13.
- Koskimies, P., & Sulkava, S. (2011). Diet of gyrfalcon (*Falcon Rusticolus* in Northern Fennoscandia. *Gyrfalcons and Ptarmigan in a Changing World – Conference Proceedings*, 177-190.
- Kvasnes, M. A., Storaas, T., Pedersen, H. C., Bjørk, S., & Nilsen, E. B. (2010). Spatial dynamics of Norwegian tetraonid populations. *Ecological Research*(25), pp. 367-374.
- Marques, F. F., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A., & Peace, A. J. (2001). Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology*(38), pp. 349-363.
- Matsuda, H., Uno, H., Tamada, K., Kaji, K., Saitoh, T., Hirakawa, H., . . . Fujimoto, T. (2002). Harvest-Based Estimation of Population Size for Sika Deer on Hokkaido Island, Japan. *Wildlife Society Bulletin*, 30(4), pp. 1160-1171.
- Merli, E., & Meriggi, A. (2006). Using harvest data to predict habitat-population relationship of the wild boar *Sus scrofa* in Northern Italy. *Acta Theriologica*, 4, pp. 383-394.
- Mossop, D. H. (2011). Long-term studies of willow ptarmigan and gyrfalcon. *Gyrfalcons and Ptarmigan in a Changing World – Conference Proceedings*, pp. 323-336.
- Myrberget, S. (1974). Variations in the Production of the Willow Grouse *Lagopus lagopus* (L.) in Norway, 1963-1972. *Ornis Scandinavica*(5), pp. 163-172.

- Mysterud, A., Meisingset, E. L., Veiberg, V., Langvatn, R., Solberg, E. J., Loe, L. E., & Stenseth, N. C. (2007). Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. *Wildlif Biology*(13), pp. 285-299.
- Neswon, S. E., Evans, K. L., Noble, D. G., Greenwood, J. J., & Gaston, K. J. (2008). Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *Journal of Applied Ecology*(45), pp. 1330–1338.
- Newborn, D., & Foster, R. (2002). Control of parasite burdens in wild red grouse *Lagopus lagopus scoticus* through the indirect application of anthelmintics. *Journal of Applied Ecology*(39), pp. 909-914.
- Nielsen, Ó. K., & Pétursson, G. (1995). Population fluctuations of gyrfalcon and rock ptarmigan: analysis of export figures from Iceland. *Wildlife Biology*(1), pp. 65-71.
- O'Brien, R. M. (2007). A Caution Regarding Rules of Thumb. *Quality & Quantity*(41), pp. 673–690.
- Official Statistics of Finland. (2012). *Hunting 2011*. Helsinki: Finnish Game and Fisheries Research institute.
- Pedersen, H. C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R. A., Svendsen, W., & Yoccoz, N. G. (2003). Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. *The Royal Society*(271), pp. 381-385.
- Plumptre, A. J. (2001). Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology*(37), pp. 356–368.
- R Development Core Team (2012) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for statistical computing. (n.d.).
- Sandercock, B. K., Nilsen, E. B., Brøseth, H., & Pedersen, H. C. (2010). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology*(80), pp. 244-258.
- Sinclair, A. R., Fryxell, J. M., & Caughley, G. (2006). *Wildlife Ecology, Conservation and Management*. Blackwell Publishing.
- Small, R. J., Marcström, Y., & Willebrand, T. (1993). Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography*(16), pp. 360–364.
- smavilt.se. (2012). Retrieved November 4., 2012, from <http://www.smavilt.se/start.htm>

- Smith, A. A. (1997). Movement, Dispersal and Survival Patterns of Swedish Willow Grouse (*Lagopus lagopus* L.). *Edward Grey Institute, Department of Zoology, University of Oxford*.
- Smith, A., & Willebrand, T. (1999). Mortality Causes and Survival Rates of Hunted and Unhunted Willow Grouse. *The Journal of Wildlife Management*(63), pp. 722-730.
- Solberg, E. J., Sæther, B. E., Strand, O., & Loison, A. (1999). Dynamics of a harvested moose population in a variable. *Journal of Animal Ecology*(68), pp. 186–204.
- Statistics Norway. (n.d.). *Jakt og fritidsfiske*. Retrieved November 5, 2012, from <http://www.ssb.no/emner/10/04/10/srjakt/tab-2012-08-08-01.html>
- Storch, I. (2007). Grouse: Status Survey and Conservation Action Plan 2006. *Gland, Switzerland: IUCN and Fordingbridge, UK: World Pheasant Association*. 114p.
- Tharme, A. P., Green, R. E., Baines, D., Bainbridge, I. P., & O'Brien, M. (2001). The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology*(38), pp. 439-457.
- Thirgood, S., Redpath, S., Newton, I., & Hudson, P. (2000). Raptors and Red Grouse: Conservation Conflicts and Management Solutions. *Conservation Biology*(14), pp. 95-104.
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., . . . Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, pp. 5–14.
- Tornberg, R. (1997). Prey selection of the goshawk *Accipiter gentilis* during the breeding season: The role of prey profitability and vulnerability. *Ornis Fennica*(74), pp. 15-28.
- Tornberg, R., Korpimäki, E., Jungell, S., & Reif, V. (2005). Delayed numerical response of goshawks to population fluctuations of forest grouse. *Oikos*(111), pp. 408–415.
- Townsend, C. R., Begon, M., & Harper, J. L. (2008). *Essentials of Ecology (3rd edition)*. Oxford: Blackwell Publishing.
- Trewhella, W. J., Harris, S., & McAllister, F. E. (1988). Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): A quantitative analysis. (25), pp. 423-434.
- Wam, H. K., Andersen, O., & Pedersen, H. C. (2013). Grouse Hunting Regulations and Hunter Typologies in Norway. *Human Dimensions of Wildlife*(18), pp. 45-57.
- Watson, A., & Moss, R. (1979). Population cycles in the Tetraonidae. *Ornis Fennica*(57), pp. 87-109.

Willebrand , T., & Hörnell, M. (2001). Understanding the effects of harvesting willow ptarmigan *Lagopus*. *Wildlife Biology*(7), pp. 205-212.

Willebrand, T., Hörnell-Willebrand, M., & Asmyhr, L. (2011). Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. *Oikos*(120), pp. 1-7.

Appendix

Year	ID	correction factor	harvest	hunting days
04/05	S	1.09	589	384
04/05	C	1.09	64	35
04/05	A	1.09	282	135
04/05	B	1.09	368	168
05/06	S	1.09	82	182
05/06	C	1.09	71	36
05/06	A	1.09	317	170
05/06	B	1.09	383	196
06/07	S	1.03	203	276
06/07	C	1.18	59	43
06/07	A	1.00	185	139
06/07	B	1.12	360	203
07/08	S	1.05	385	304
07/08	C	1.14	25	27
07/08	A	1.09	215	238
07/08	B	1.09	527	284
08/09	S	1.14	146	227
08/09	C	1.13	15	16
08/09	A	1.24	153	181

08/09	B	1.10	536	289
10/11	S	1.02	312	179
10/11	C	1.09	57	46
10/11	B	1.02	215	238

Appendix A:

Year	Total reports	Dog training reports	missing reports	Faulty reports
04/05	15113	4	0	900
05/06	13790	1241	19	258
06/07	14383	876	1709	297
07/08	15328	1163	1846	480
08/09	14864	1081	2128	218
09/10	3920	686	388	42
10/11	11025	1397	583	211

Appendix B